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# The parameters of grain filling and yield components in common wheat (*Triticum aestivum* L.) and durum wheat (*Triticum turgidum* L. var. *durum*)

**Research Article**

Milka D. Brdar[1*], Marija M. Kraljević-Balalić[2], Borislav Đ. Kobiljski[1]

[1] *Research Institute of Field and Vegetable Crops 21000 Novi Sad, Republic of Serbia*

[2] *Faculty of Agriculture, University of Novi Sad, 21000 Novi Sad, Republic of Serbia*

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**Abstract:** Final grain dry weight, a component of yield in wheat, is dependent on the duration and the rate of grain filling. The purpose of the study was to compare the grain filling patterns between common wheat, (*Triticum aestivum* L.), and durum wheat, (*Triticum turgidum* L. var. *durum*), and investigate relationships among grain filling parameters, yield components and the yield itself. The most important variables in differentiating among grain filling curves were final grain dry weight (W) for common wheat genotypes and grain filling rate (R) for durum wheat genotypes; however, in all cases the sets of variables important in differentiating among grain filling curves were extended to either two or all three parameters. Furthermore, in one out of three environmental conditions and for both groups of genotypes, the most important parameter in the set was grain filling duration (T). It indicates significant impact of environmental conditions on dry matter accumulation and the mutual effect of grain filling duration and its rate on the final grain dry weight. The medium early anthesis date could be associated with further grain weight and yield improvements in wheat. Grain filling of earlier genotypes occurs in more temperate environments, which provides enough time for gradual grain fill and avoids the extremes of temperature and the stress of dry conditions.

**Keywords:** *Wheat • Grain filling • Yield*



## 1. Introduction

The grain yield of both common wheat (*Triticum aestivum* L.), and durum wheat (*Triticum turgidum* L. var. *durum*), depends on three components: grain weight, number of grains per spike and number of spikes per unit area. Grain filling is the period between anthesis and maturity; during that time, the accumulation of dry matter and its partitioning into grain was determined [1]. Grain weight is a result of the grain filling process, which is defined by two parameters: grain filling duration and rate. Grain filling duration can be expressed as the time between anthesis and physiological maturity, beyond the point where there is no significant increase in grain dry matter, [2] and the time between anthesis and harvest maturity (13% moisture in grains) [3]. The most important goal in wheat breeding is to increase grain yield and quality. As a wheat yield component, final grain weight is the grain weight determined after harvest. Southern Europe is mostly arid or semiarid region, and it is an area of temperature stress and the late-season rise of temperature has been known to adversely affect grain yield and quality [4]. For that purposes we choosed to express grain filling duration as the time between anthesis and harvest maturity.

Several statistical methods have been used in attempts to describe grain filling. Average grain filling rate were calculated as the ratio of maximum grain weight to grain filling duration [5,6], which were estimated from quadratic polynomial curves. Furthermore, [7] estimated

* *E-mail: milkabrdar@yahoo.com*

maximum grain weight and grain filling duration was determined from cubic polynomials. Linear regression [8] has been employed to estimate grain filling rate and the intersection of two regression lines has been used to estimate grain filling duration. Logistic models were found to be more appropriate in describing wheat grain growth [9]. Therefore, stepwise multivariate analysis-MANOVA of nonlinear regression estimated grain filling parameters was proposed as the most suitable statistical method [3,10]. Univariate analysis of variance (ANOVA) is sometimes used to differentiate among growth curves, but, MANOVA proved to be more appropriate for analyzing growth curve parameters. It clarifies the relative importance of the various parameters in a growth curve.

Temperature is the most important environmental factor affecting grain filling parameters and grain weight [5,7,11]. Each 1°C increase in the main daily temperature above optimum (12-15°C) for grain filling, resulted in the decrease of approximately 2.8 mg and 3.1 days in grain weight and grain filling duration [12]. However, genotypic differences among wheat genotypes exist for both the grain filling duration and its rate [13,14] and can be exploited for the purpose of creating high-yielding cultivars. By comparing the variation in different species, a valuable tool in identifying traits has been proven to be useful in plant breeding [15].

A better understanding of the relationships between plant development in various climatic conditions and yield, may help breeding and agronomic efforts to improve and stabilize yield in wheat. This study was undertaken in order to compare grain filling patterns between groups of common and durum wheat genotypes, and investigate relationships among grain filling parameters, yield components and yield. To detect genotypes suitable for further breeding programs, growth analysis may provide important information [10].

## 2. Experimental Procedures

The experimental material consisted of three common winter wheat cultivars (Pobeda, Renesansa, and Evropa 90), created at the Research Institute of Field and Vegetable Crops in Novi Sad, Republic of Serbia, and three durum wheat genotypes (Durumko, Neodur, NSD 81/98). Durumko is a facultative cultivar and NSD 81/98 represents a perspective winter line, both originating from Novi Sad. Neodur is a French winter cultivar. Those genotypes were chosen for the study because they possessed different patterns of grain filling and different relationships among yield components, although all of them are capable of producing high yields.

The trial was conducted at the experimental field, Rimski Šančevi, Novi Sad (45° 20' N, 19° 51' E, 84 meters asl) during the growing seasons in 2000, 2001 and 2002. The experiment was conducted in a randomized blocks, with four replications. The dimension of the main plots were 5 m². Standard agrotechnical procedures were applied. The Rimski Šančevi meteorological station data were used, and the mean daily temperatures, the total temperatures and of the total amount of precipitation in May and June are listed in Table 1.

| Year | 2000 | 2001 | 2002 |
|---|---|---|---|
| Sum of temperatures | 1214.5 | 1098.5 | 1245 |
| Average daily temperature | 20 | 18 | 20.4 |
| Sum of precipitation | 67 | 308 | 114 |

**Table 1.** The sum of temperatures (°C), average daily temperature (°C) and sum of precipitation (mm) in May and June for seasons of 2000, 2001 and 2002 (Rimski Šančevi meteorological station data, Novi Sad).

Sampling was initiated fourteen days after anthesis and continued at 7-day intervals in first three weeks, and approximately two-day intervals afterwards, until harvest maturity (13% moisture in grain). Random samples of 20 spikes per plot were harvested on each sampling date, and were selected in four repeated trial runs. Differences regarding the occurrence of anthesis, grain filling duration, and final grain weight within spikes, have been reported by [16]. To assure uniformity, ten grains from the middle of each of the twenty spikes were removed and oven dried at 80°C for 24 hours. The grains were weighed before and after drying. The anthesis date (AD) was expressed as the number of days from 1 January to anthesis, and observed grain filling duration was calculated as number of days from anthesis to harvest maturity. Dry matter accumulation was expressed as a function of accumulated growing degree days (GDD) from anthesis, because the use of GDD rather than days provides a better fit to the grain filling curves [3]. Growing degree days were calculated as a sum of daily degree days ($T_n$), which was determined by the formula: $T_n=\{(T_{max}+T_{min})/2\}-T_b$, where $T_{max}$ and $T_{min}$ are the maximum and minimum daily temperatures, and $T_b$ is the base temperature (0°C). Below the base temperature plants are unable to develop [17].

The data from each plot were fitted by a nonlinear regression to a logistic curve:

$y=W/\{1+\exp(B–Cx)\}$ (Eq.1.),

proposed by [3].

Observed average grain weight (mg) is represented with y and x represents accumulated GDD from anthesis. The estimate of final grain weight (mg) is W, B was correlated to both duration and rate of grain filling, and C was correlated to the grain filling rate. Estimates of W, B and C were determined by nonlinear regression, using the STATISTICA 7.0 software package. The

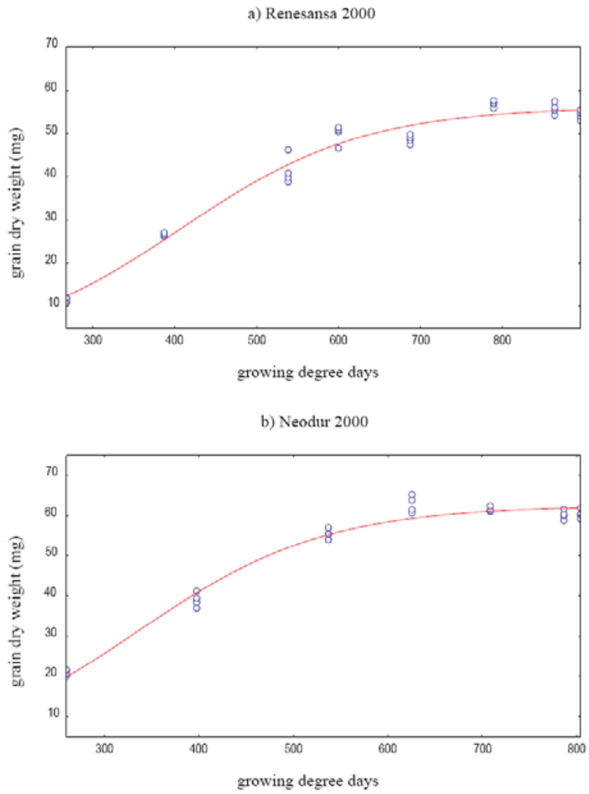


**Figure 1.** The relationship between grain dry weight and accumulated growing degree days during grain filling in a) common wheat cultivar Renesansa and b) durum wheat cultivar Neodur in 2000.

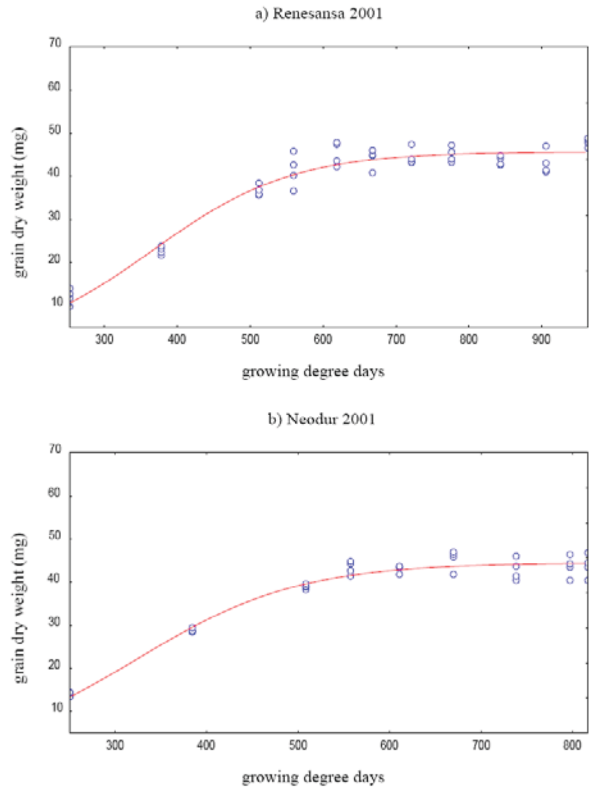


**Figure 2.** The relationship between grain dry weight and accumulated growing degree days during grain filling in a) common wheat cultivar Renesansa and b) durum wheat cultivar Neodur in 2001.

maximum rate of grain filling (R) was calculated using the derivative of the logistic curve: dy/dx=Cy(W–y)/W, where dy/dx represents the instantaneous grain filling rate. This value reaches a maximum when y=0.5W, so the maximum rate of grain filling can be calculated as R=CW/4. Theoretically, grain dry weight will never reach its asymptotic maximum W, so grain filling was considered to be complete when y=0.95W. Based on this assumption, an estimate of the grain filling duration (T) was calculated by substituting 0.95W for y in the derivative of the logistic curve and solving for x using the formula, x=T=(B+2.944)/C.

The variables W, R and T were first analyzed by ANOVA. Since all three variables define the shape of each growth curve, the stepwise MANOVA method described by [10] was considered to be a more appropriate one than ANOVA for comparisons of growth curves. The procedure was used in order to determine which of the estimated variables (W, R, T) were most important in assessing the grain filling curves. The variable with the lowest Wilks' λ-value was considered first. It is the most significant variable. Further, the most significant pair of variables including the first variable was considered. Finally, the set can be extended to all three variables. Each additional variable of the set was considered to be significant only if the new variable adds information not already contained in the previous set. A test of significance of a new variable was facilitated through the calculation of conditional λ-values. For example, extending the set (W) by T provides additional information if λ(T\W) was significant. The conditional set λ(T\W) represents the effect of T after removal of the effects of the covariable W and can be calculated from unconditional λ-values as λ(T\W)=λ(WT)/λ(W). If this λ-value was significant, the importance of adding the next variable (R) can be determined by calculating the λ-value for R after removal of the effects of W and T: λ(R\WT)=λ(WRT)/λ(WT) [3]. All calculations, including explanations regarding degrees of freedom given in various tables, were described in details together with a numerical example in [10].

Yield components (final grain dry weight-GW (mg), number of grains per spike-NG, and the number of spikes per $m^2$-NS) and yield-Y ($kg/m^2$) were analyzed after the harvest. The number of grains per spike were expressed as the average number of grains on ten randomly chosen spikes per plot. The spikes were collected at harvest maturity, threshed by hand, and the

| | 2000 | | | 2001 | | | 2002 | | |
|---|---|---|---|---|---|---|---|---|---|
| | W | B | C | W | B | C | W | B | C |
| | Common wheat genotypes | | | | | | | | |
| Pobeda | 48.82 | 4.8226 | 0.0119 | 39.94 | 5.1817 | 0.0145 | 53.17 | 2.5654 | 0.0077 |
| SE | 1.06 | 0.7542 | 0.0018 | 0.63 | 0.7382 | 0.0020 | 2.49 | 0.2409 | 0.0010 |
| Renesansa | 56.08 | 3.6618 | 0.0090 | 45.73 | 3.8293 | 0.0104 | 53.21 | 3.2518 | 0.0089 |
| SE | 0.96 | 0.2686 | 0.0007 | 0.77 | 0.4884 | 0.0013 | 2.59 | 0.6019 | 0.0018 |
| Evropa 90 | 50.46 | 4.1020 | 0.0103 | 39.82 | 4.2136 | 0.0116 | 47.39 | 2.9587 | 0.0083 |
| SE | 0.98 | 0.4337 | 0.0011 | 0.73 | 0.5673 | 0.0016 | 1.39 | 0.3407 | 0.0011 |
| | Durum wheat genotypes | | | | | | | | |
| Durumko | 62.00 | 2.8188 | 0.0109 | 39.86 | 3.0593 | 0.0098 | 54.81 | 3.4107 | 0.0093 |
| SE | 0.54 | 0.2138 | 0.0008 | 1.06 | 0.6223 | 0.0020 | 2.00 | 0.5643 | 0.0018 |
| Neodur | 62.40 | 3.3914 | 0.0101 | 44.48 | 3.6918 | 0.0114 | 56.31 | 3.2948 | 0.0094 |
| SE | 0.75 | 0.2388 | 0.0007 | 0.62 | 0.3839 | 0.0012 | 2.81 | 0.5769 | 0.0017 |
| NSD81/98 | 60.18 | 4.4925 | 0.0103 | 42.01 | 4.1650 | 0.0117 | 53.11 | 3.3439 | 0.0098 |
| SE | 2.42 | 1.1229 | 0.0028 | 0.82 | 0.6849 | 0.0019 | 2.27 | 0.8257 | 0.0026 |

**Table 2.** Mean values and standard errors (SE) of nonlinear regression estimated (Eq. 1.) parameters W (final grain dry weight-mg), B and C in 3 common and 3 durum wheat genotypes in 2000, 2001 and 2002.

| | AD | GW | W | R | T | D | NG | NS | Y |
|---|---|---|---|---|---|---|---|---|---|
| | days | mg | mg | mg/GDD | GDD | days | - | - | kg/m2 |
| Genotypes | | | | | | | | | |
| Pobeda | 131.7 a | 44.3 a | 47.3 a | 0.1310 a | 642.0 a | 44.7 a | 42.2 ac | 896.0 a | 1.67 a |
| Renesansa | 129.7 b | 51.2 bd | 51.7 b | 0.1216 b | 693.0 b | 45.3 b | 44.5 b | 890.7 a | 2.00 b |
| Evropa 90 | 131.0 c | 42.6 c | 45.9 a | 0.1146 c | 670.5 c | 43.7 c | 44.2 ab | 890.7 a | 1.66 a |
| Durumko | 136.7 d | 50.9 b | 52.2 b | 0.1315 ad | 609.5 d | 40.3 d | 45.9 b | 704.0 b | 1.57 ac |
| Neodur | 135.0 e | 52.8 d | 54.4 c | 0.1390 e | 624.5 d | 40.7 d | 40.9 c | 696.0 b | 1.37 c |
| NSD81/98 | 130.0 b | 49.6 b | 51.8 b | 0.1361 de | 657.5 ac | 44.7 a | 52.0 d | 668.0 b | 1.51 ac |
| Years | | | | | | | | | |
| 2000 | 129.0 a | 54.9 a | 56.7 a | 0.1474 a | 658.5 a | 42.8 a | 44.8 a | 754.7 a | 1.69 a |
| 2001 | 137.0 b | 40.2 b | 42.0 b | 0.1212 b | 605.5 b | 48.4 b | 48.2 b | 832.0 a | 1.62 a |
| 2002 | 132.0 c | 50.5 c | 53.0 c | 0.1184 b | 684.5 c | 39.3 c | 41.8 c | 786.0 a | 1.57 a |

**Table 3.** Anthesis date (AD), observed (GW) and estimated (W) final grain dry weight, estimated maximum grain filling rate (R), estimated (T) and observed (D) grain filling duration, number of grains/spike (NG), number of spikes/m2 (NS) and yield (Y) for 3 common and 3 durum wheat genotypes for three seasons (2000, 2001, 2002).

*a-f values within columns followed by the same letter do not differ significantly at the 0.05 level of probability according to LSD test*

number of grains were determined with an electronic counter. The number of spikes per $m^2$ were determined prior to harvest, by counting the number of spikes in a 0.5 $m^2$ central section of each plot.

Correlation coefficients were calculated in order to investigate possible relationships among grain filling parameters, yield components and yield.

## 3. Results and Discussion

The logistic curve provided a good fit to the grain filling data for all six genotypes and three environments (Figure 1, 2 and 3, e. g.) with $R^2$ values exceeding 0.94 in all cases (data not shown).

The equation $y=W/\{1+\exp(B-Cx)\}$ was used to estimate grain filling parameters (duration-T and maximum rate of grain filling-R) and final grain weight-W. Standard errors for the fitted equations together with W, B and C values are listed in Table 2.

The logistic equation overestimated final grain dry weight (W) in relation to observed (GW), but provided similar ranking for genotypes, which is in accordance with results obtained by [17]. The ranking of genotypes concerning nonlinear regression, estimated (T), and observed (D) grain filling duration, were also similar. In contrast, the year averages of T and D were in inverse proportion, probably caused by the difference in method of measurement (Table 3). The nonlinear

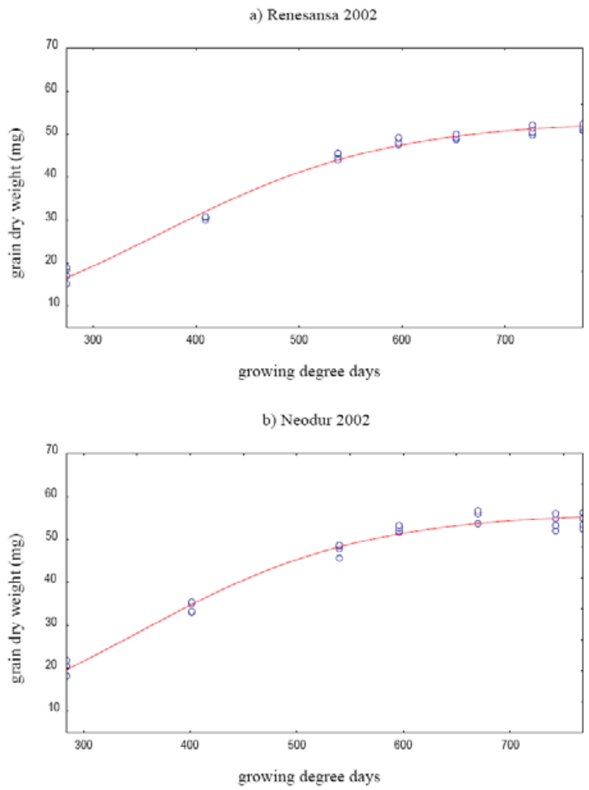


**Figure 3.** The relationship between grain dry weight and accumulated growing degree days during grain filling in a) common wheat cultivar Renesansa and b) durum wheat cultivar Neodur in 2002.

regression estimated grain filling duration is expressed in accumulated growing degree days from anthesis to maturity (°C), and it is based on the logistic curve, largely determined by final grain dry weight. Observed grain filling duration is the time in calendar days from anthesis to harvest maturity (13% moisture in grains). The shortest grain filling duration, measured in GDD, noted for 2001), was due to the unusually low average daily temperatures in May and June. Measured in time units, the same year was characterized by extremely slow grain filling, precisely because the low average daily temperatures and high sum of precipitation that occurred during grain filling. Conversely, the longest grain filling duration measured in GDD and the shortest grain filling duration measured in days (noted for 2002), the season characterized by 2.4°C higher average daily temperature than in the table for 2001 (Table 1). Therefore, high temperatures hasten grain filling as expressed in time units. However, the same conditions means longer grain filling as measured in GDD units.

The combined ANOVA of all trials demonstrated differences among both common and durum wheat genotypes and environments for all nonlinear regression estimated grain filling parameters. The genotype-environment interactions were also significant in almost all cases. The only exception was the insignificant genotype-environment interaction involving the variable W in group of durum wheat genotypes (data not shown).

Analyses of variance conducted on individual trials showed differences among common wheat genotypes for all estimated grain filling parameters in all environments, except for T in 2002. Differences among durum wheat genotypes occurred only for the parameter T in 2000, and for the parameters W and R in 2001. Analyses of variance failed to detect differences among those genotypes regarding grain filling parameters in 2002 (Table 4). Therefore, univariate analyses of variance imply that final grain dry weight and grain filling rate were the most important parameters in defining grain filling differences among common wheat genotypes, although grain filling duration was also important in two out of three environments. For durum wheat, according to ANOVA, the grain filling duration and the final grain dry weight were the most important parameters in differentiating among genotypes in two out of three environments, while the grain filling rate was also important in one environment.

Multivariate analysis of variance was used for each trial in order to define the significance of genotypic effects for the set of estimated variables (W, R, T) and all their possible subsets (Table 4). The method of stepwise MANOVA [18] was used in order to determine the smallest set of variables (final set) that adds information to genotypic grain filling curves.

The final grain dry weight (W) for common wheat genotypes, and grain filling duration (T) for durum wheat genotypes, were the parameters with the smallest λ-values in 2000. Therefore, of all these three parameters, W and T were the most important in differentiating among grain filling curves, although in cases of both common and durum wheat, the sets were extended to all three parameters. The final set for common wheat genotypes consisted of T and R in 2001 and of all three parameters, with W as the most important, in 2002. For durum wheat genotypes, the grain filling rate (R) was the parameter with the smallest λ-value in both 2001 and 2002. The set was extended to all three parameters in 2001 and to parameter W in 2002 (Table 5). Therefore, the results obtained from stepwise multivariate analyses indicate that final grain dry weight (W) for common wheat genotypes and grain filling rate (R) for durum wheat genotypes are the most important variables in differentiating among grain filling curves. However, in all three environments, for both common and durum wheat genotypes, the sets were extended to at least two or sometimes all three parameters.

| | Common wheat genotypes | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 2000 | | | 2001 | | | 2002 | | |
| set | λ | df | F | λ | df | F | λ | df | F |
| W,R,T | 0.0069 | 6, 14 | 25.76** | 0.0092 | 6, 14 | 21.93** | 0.0003 | 6, 14 | 145.19** |
| W,R | 0.0713 | 4, 16 | 10.98** | 0.0157 | 4, 16 | 27.95** | 0.0046 | 4, 16 | 55.01** |
| W,T | 0.1199 | 4, 16 | 7.55** | 0.0299 | 4, 16 | 19.14** | 0.0025 | 4, 16 | 75.94** |
| R,T | 0.1081 | 4, 16 | 8.17** | 0.0127 | 4, 16 | 31.43** | 0.0326 | 4, 16 | 18.15** |
| W | 0.1461 | 2, 9 | 26.29** | 0.2554 | 2, 9 | 13.12** | 0.1190 | 2, 9 | 33.31** |
| R | 0.3889 | 2, 9 | 7.07** | 0.0720 | 2, 9 | 58.01** | 0.1262 | 2, 9 | 31.15** |
| T | 0.2675 | 2, 9 | 12.32** | 0.0694 | 2, 9 | 60.35** | 0.7426 | 2, 9 | 1.56 ns |
| | Durum wheat genotypes | | | | | | | | |
| | 2000 | | | 2001 | | | 2002 | | |
| set | λ | df | F | λ | df | F | λ | df | F |
| W,R,T | 0.0016 | 6, 14 | 55.15** | 0.0027 | 6, 14 | 42.19** | 0.0495 | 6, 14 | 8.15** |
| W,R | 0.4589 | 4, 16 | 1.90 ns | 0.0583 | 4, 16 | 12.57** | 0.4086 | 4, 16 | 2.26 ns |
| W,T | 0.0395 | 4, 16 | 16.20** | 0.0981 | 4, 16 | 8.77** | 0.2959 | 4, 16 | 3.35* |
| R,T | 0.0082 | 4, 16 | 40.30** | 0.0454 | 4, 16 | 14.78** | 0.1871 | 4, 16 | 5.25** |
| W | 0.6627 | 2, 9 | 2.29 ns | 0.4803 | 2, 9 | 4.87* | 0.7413 | 2, 9 | 1.57 ns |
| R | 0.6550 | 2, 9 | 2.37 ns | 0.0896 | 2, 9 | 45.73** | 0.7895 | 2, 9 | 1.20 ns |
| T | 0.0488 | 2, 9 | 87.73** | 0.6923 | 2, 9 | 2.00 ns | 0.6347 | 2, 9 | 2.59 ns |

**Table 4.** Summary of tests of genotype effects in multivariate analyses of variance of final grain dry weight (W), maximum rate of grain filling (R) and duration of grain filling (T) in growing degree days from anthesis to 0.95W, for three common and three durum wheat genotypes.

*df-degrees of freedom; λ-Wilks' λ criterion; ns, *, **-insignificant, significant at the 0.05 and 0.01 levels of probability, respectively*

| | Common wheat genotypes | | | | |
|---|---|---|---|---|---|
| environment | conditional set | Wilks' λ | df | F | final set |
| 2000 | W | 0.1461 | 2, 9 | 26.29** | |
| | R \ W | 0.4876 | 2, 8 | 4.20 ns | |
| | T \ W | 0.8204 | 2, 8 | 0.88 ns | |
| | RT \ W | 0.0472 | 4, 14 | 12.61** | W, R, T |
| 2001 | T | 0.0694 | 2, 9 | 60.35** | |
| | R \ T | 0.1837 | 2, 8 | 17.78** | |
| | W \ TR | 0.7255 | 2, 7 | 1.32 ns | T, R |
| 2002 | W | 0.1190 | 2, 9 | 33.31** | |
| | T \ W | 0.0210 | 2, 8 | 186.19** | |
| | R \ WT | 0.0999 | 2, 7 | 31.54** | W, T, R |
| | Durum wheat genotypes | | | | |
| environment | conditional set | Wilks' λ | df | F | final set |
| 2000 | T | 0.0488 | 2, 9 | 87.73** | |
| | R \ T | 0.1671 | 2, 8 | 19.93** | |
| | W \ TR | 0.2020 | 2, 7 | 13.83** | T, R, W |
| 2001 | R | 0.0896 | 2, 9 | 45.73** | |
| | T \ R | 0.5063 | 2, 8 | 3.90 ns | |
| | W \ R | 0.6503 | 2, 8 | 2.15 ns | |
| | TW \ R | 0.0306 | 4, 14 | 16.49** | R, T, W |
| 2002 | T | 0.6347 | 2, 9 | 2.59 ns | |
| | R \ T | 0.2948 | 2, 8 | 9.57** | |
| | W \ TR | 0.2646 | 2, 7 | 9.73** | R, W |

**Table 5.** Determination of the smallest set of estimated variables (final grain dry weight (W), maximum rate (R) and duration (T) of grain filling) required to completely characterize the grain filling curves of 3 common and 3 durum wheat genotypes.

*λ-Wilks' λ criterion; df-degrees of freedom; ns, *, **-insignificant, significant at the 0.05 and 0.01 levels of probability, respectively*

| | W | R | T | NG | NS | Y |
|---|---|---|---|---|---|---|
| AD | -0.44** | ns | -0.71** | ns | ns | ns |
| W | | 0.55** | 0.29* | -0.24* | -0.33** | ns |
| R | | | -0.41** | ns | -0.23* | ns |
| T | | | | ns | ns | ns |
| NG | | | | | ns | ns |
| NS | | | | | | 0.78** |

**Table 6.** Correlation coefficients among anthesis date (AD), estimated final grain dry weight (W), maximum rate (R) and duration (T) of grain filling, number of grains/spike (NG), number of spikes/m2 (NS) and yield (Y) for three common and three durum wheat genotypes.

*ns, *, **-insignificant, significant at the 0.05 and 0.01 levels of probability, respectively*

During the three year period, the highest final grain dry weight among common wheat genotypes had cultivar Renesansa. Renesansa had the longest grain filling duration and the highest yield of all six genotypes studied, opposed to the results obtained by [3] and [17]. They reported that genotypes with the highest grain dry weight also have the shortest grain filling periods and the highest grain filling rates. In contrast, among durum wheat genotypes, the highest final grain dry weight was achieved by Neodur, which had the highest grain filling rate, but also the lowest yield among all six analyzed genotypes (Table 3).

Correlation coefficients were calculated in order to investigate the relationship among grain filling parameters, yield components and yield. Final grain dry weight (W) was positively correlated with both grain filling duration (T) and rate (R), similar to the results obtained by [7]. R and T were negatively correlated, in accordance to the results reported by a number of authors [e. g. 2]. W was also negatively correlated with number of grains per spike (NG), and the number of spikes per $m^2$ (NS). Compensatory effects among yield components were found to be common and are well documented [e. g. 19], especially under warmer weather conditions [20]. The only positive correlation noted for yield (Y) was with NS (Table 6), which is in accordance with research performed by [21] and [22], who found that yield differences among durum wheat genotypes mainly depended on different number of grains per unit area. Similar results are reported for common wheat [23].

The number of grains was determined in relatively early phases of plant development [24] and the after anthesis yield depended on grain weight [16]. In our study, similar to the results obtained by [4], earlier genotypes had larger grains and longer grain filling duration (Table 6). Despite negative correlation between R and T, early anthesis did not affect grain filling rate. The advantage of earlier genotypes could be explained by the fact that grain filling of earlier genotypes occurs in an environment favorable enough to avoid yield losses due to dry and temperature stresses, common in our region. Therefore, moderately early anthesis dates could be associated with further grain weight and yield improvements in wheat.

# 4. Conclusions

MANOVA of nonlinear regression estimated grain filling parameters showed that final grain dry weight (W) for common wheat genotypes and grain filling rate (R) for durum wheat genotypes were the most significant variables in differentiating among grain filling curves. However, in one out of three environments, for both durum and common wheat genotypes, the most important variable was duration of grain filling (T), and the sets of variables important in differentiating among grain filling curves were extended to two or even all three variables in all cases.

Final grain dry weight positively correlated with both grain filling duration and rate, and the number of spikes per $m^2$ negatively correlated with grain filling rate. The rate and duration of grain filling were negatively correlated. Compensatory effects among yield components were revealed, and the yield positively correlated only with the number of spikes per $m^2$.

These results demonstrate that the rate and duration of grain filling cannot be studied separately, owing to their mutual impact on dry matter accumulation, which is not the same in diverse environments.

Early anthesis enables more a suitable environment for grain filling. It maintains enough time for gradual grain fill and avoids of extremes of dry climate and temperature stresses.

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